

THE FIRST MESOZOIC CHONDROPHORINE (MEDUSOID HYDROZOAN), FROM THE LOWER CRETACEOUS OF JAPAN

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ABSTRACT. Floating jellyfish-like hydrozoans belonging to the Suborder Chondrophorina are a little known but distinctive group extending back to the Precambrian with sporadic occurrences in the Palaeozoic. Their absence from post-Carboniferous rocks was puzzling, considering their abundance and wide distribution today. *Palaeophacmaea annulata* (Yokoyama), from the lower Cretaceous (Barremian) of Japan, is reinterpreted as the first known example of a chondrophorine fossil from the Mesozoic. The species was previously considered to be a patelliform gastropod. The remarkable similarity of chondrophorine pneumatophores to some univalved molluscs complicates precise identification. Possible criteria to aid in distinguishing these little-known fossils are discussed.

CHONDROPHORINES are floating jellyfish-like hydrozoans represented in today's oceans by the widely distributed *Veleva* and *Porpita*. *Veleva* employs a fixed sail as its principal means of propulsion and such open-sea mariners are accordingly referred to as 'by-the-wind sailors'. Whole flotillas of these organisms are frequently driven onshore by strong wind. *Porpita*, another chondrophorine, lacks a sail but follows a similar planktonic life-style. Details of the anatomy and ecology of both organisms were given by Hyman (1940).

Although thought of as soft-bodied jellyfish, chondrophorines actually secrete within their coenosarc tissues a tough, gas-filled, chitinoid float structure, the pneumatophore. In *Veleva* these convex structures consist of a concentric series of closely adpressed gas chambers that frequently wash up in great abundance on many beaches. Such pneumatophores are hard but flexible and possess some potential for preservation. As demonstrated for some well-preserved Devonian examples, the disc-shaped pneumatophore can provide a hard surface for the attachment of epifauna (Yochelson *et al.* 1983). Sinking, burial, and compression of the concentric gas chambers may produce fossils strikingly reminiscent of some mollusc shells.

The conservative nature of chondrophorine evolution is readily apparent when Silurian or even Precambrian (Wade 1971) examples are compared with their living counterparts. During their long existence, they have undergone very little elaboration of their basic morphology. *Plectodiscus* Ruedemann, for example, is similar in both hard and soft parts to living *Veleva* and ranges from late Silurian to middle Pennsylvanian with little morphological change.

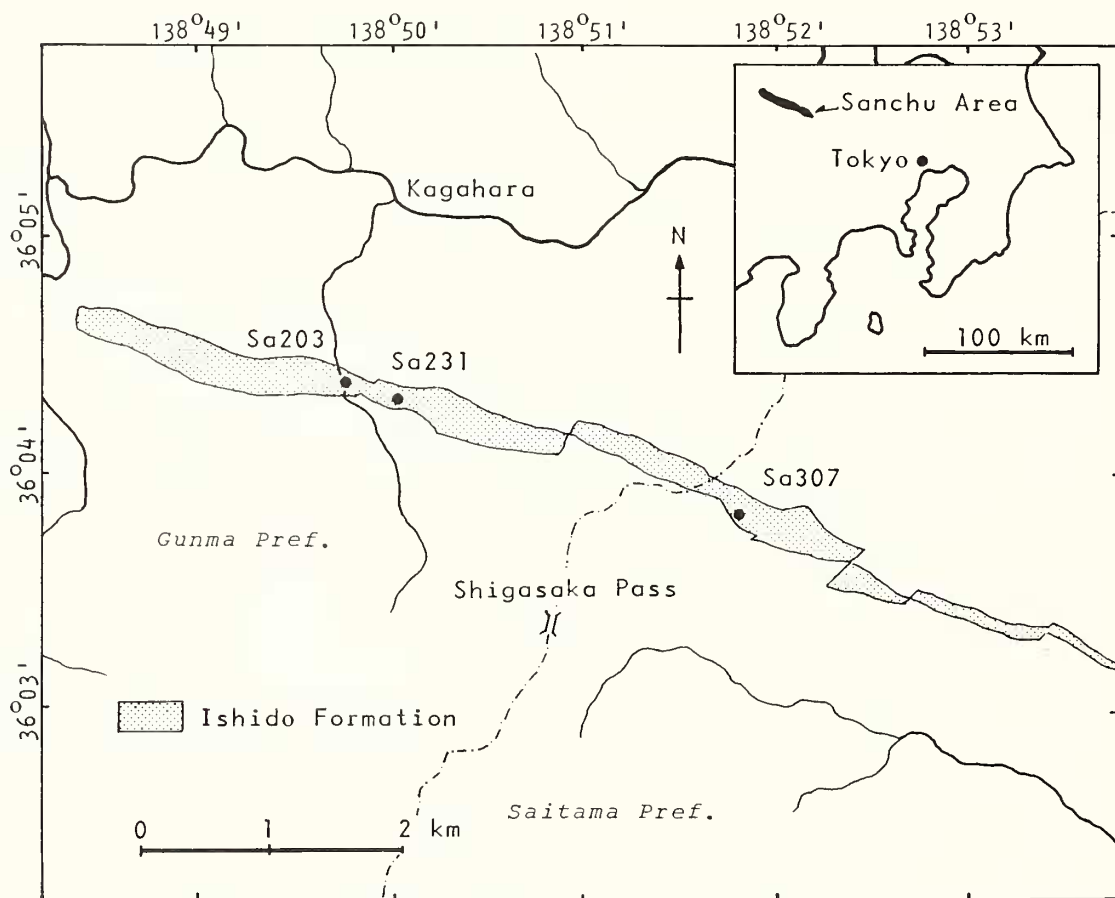
Although abundant today, the fossil record of chondrophorines is exceedingly sparse and sporadic. Only sixteen occurrences have been reported, ranging from the late Precambrian Ediacara fauna to the Carboniferous (Stanley 1982). Despite extensive palaeontological investigations of post-Carboniferous strata, no examples have been reported previously. The apparent absence of chondrophorines during this 300 MY interval is very puzzling.

We describe the first post-Carboniferous chondrophorine which comes from the lower Cretaceous of Japan and appears related to earlier examples in the lower Ordovician and Precambrian. Previously classified as molluscs, these fossils are now identified as chondrophorines.

STRATIGRAPHY AND PALAEOECOLOGY

Stratigraphic occurrence

The chondrophorine comes from localities Sa203, Sa231, Sa307 (text-fig. 1). It occurs in the upper part of the Ishido Formation in the Sanchu area of Japan (text-fig. 2). The specimens were collected by M. Matsukawa and K. Takei during geologic studies in the Sanchu area. The Ishido Formation is a fining-upwards sequence, with coarse-grained deposits grading upwards into fine-grained sandstone, which locally alternates with black shale. Localities Sa203 and Sa231 (text-fig. 1) consist of very fine-grained calcareous sandstone and locality Sa307 is composed of very fine-grained calcareous sandstone and black shale. According to Matsukawa (1977), the fossil localities in the upper fine-grained facies of the Ishido Formation are generally of muddy facies.



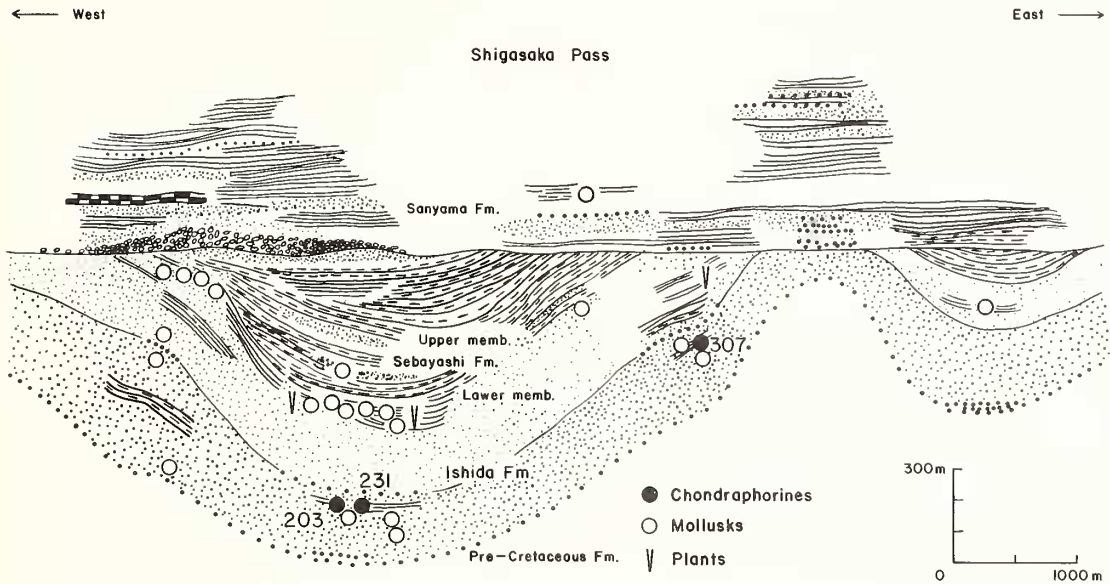
TEXT-FIG. 1. Locality map of the Sanchu area of Japan showing locations of chondrophorine fossils described in text. Numbers refer to localities.

Geological age

According to Obata *et al.* (1976), the upper part of the Ishido Formation is upper Barremian in age as shown by the occurrence of the ammonites *Barremites* (*Barremites*) aff. *stretostoma* (Uhlig), *Heteroceras* (*Heteroceras*) aff. *astieri* D'Orbigny, and *Pseudohaploceras otsukai* (Yabe and Nagao).

Palaeoecology and associated fauna

Locality Sa307 yields abundant bivalves: *Astarte (Astarte) subsenecta*, *A. (Yabea) shinanoensis*, *Entolium sauchuensis*, *Gervillaria haradae*, *Grammatodon (Nanonavis) yokoyamai*, *Pterotrigonia (Pterotrigonia) hokkaidoana*, *P. (P.) pociliformis*, *Lycettia* sp., undetermined species of scaphopods, and one species of ammonite *Barremites (Barremites)* sp. Many trigoniid bivalves occur in direct association with the chondrophorines. Numano and Nakano (1965) interpreted *Pterotrigonia* as inhabiting calm bottoms somewhat offshore. Alternatively, Tashiro and Matsuda (1982) viewed this bivalve as inhabiting a shallow sea near the tidal zone.



TEXT-FIG. 2. Geological cross-section showing the stratigraphic succession of Cretaceous rocks in the eastern part of the Sanchu 'Graben' and location of fossils including chondrophorine (after Matsukawa 1977).

Locality Sa203 contains nine taxa of uncoiled ammonites: *Kabylites* (?), *Acrioceras* aff. *tabarelli*, *Lytocrioceras* (?) *furcatum*, *L.* (?) sp., *Hamitoceras* (?) sp., *Heteroceras* sp., *H.* (?) sp., *Anahamulina* aff. *subcylindrica*, *A.* sp.; seven species of coiled ammonites: *Phyllopacyceras* aff. *infundibulum*, *Calliphylloceras* (?) sp., *Aconeceras* sp., *Barremites (Barremites)* aff. *strettostoma*, *B. (B.)* aff. *difficilis*, *B. (B.)* sp., *Pseudohaploceras* (?) *otsukai*, and one species of nautiloid *Cymatoceras* aff. *neocomiensis*. The depth distributions of the Barremian species of phylloceratids, ancyloceratids, ptychoceratids, desmoceratids, and oppelliids are uncertain. We infer depth distributions of these ammonites in the infraneritic zone between 36 and 180 m (Scott 1940) or in an intermediate facies between inshore shallow water and offshore deep water, based on the abundant occurrences of heteromorphic ammonites (Tanabe 1979).

Environment of deposition

The Ishido Formation is regarded as a transgressive deposit with a basal conglomerate. The upper part of the Ishido Formation yielding the chondrophorines represents a fine-grained, 'muddy' facies. Sandstone of the Ishido Formation in the northern sub-belts is characterized largely by a feldspathic greywacke, the clasts composed largely of chert (Takei 1980). These deposits received sediment from the north and the sedimentary basin is thought to have been close to land areas and of moderate depth. The interval yielding the chondrophorine fossil is a quiet water, transgressive stage and both palaeontological and sedimentological data are consistent with a shallow-water, predominantly fine-grained clastic sediment substrate.

PRESERVATION AND TAPHONOMY

A review of the small number of Palaeozoic chondrophorine occurrences shows that depending on the original shape, nature of enclosing sediments, and type of preservation, the configuration of the pneumatophore or disc can vary from totally flattened to a strong, cap-like convexity (Stanley 1982). After some post-mortem floating, their gas-filled pneumatophores presumably became waterlogged and sank. Abundant remains of a whole flotilla of fossil velellids have been reported from deep basinal rocks of early Carboniferous age (Stanley and Yancey in press), but examples of very shallow-water origin are also known (Yochelson and Stanley 1981). Living *Velella* occurs in great concentrations and is frequently driven landward by prevailing winds to become beached and concentrated on the strand line (Yochelson *et al.* 1983). Thus chondrophorine remains would be expected to occur throughout a wide variety of near-shore to offshore facies types and they may be locally concentrated.

The rarity of the Ishido specimens, coupled with their occurrence in relatively near-shore facies of presumed low-energy and moderate depth, suggests that these chondrophorines did not become beached but sank individually, in quiet waters a short distance offshore. The vague concentric outlines and convex shapes of some of the pneumatophores (Pl. 10, fig. 2) may have resulted from infilling of pneumatocyst chambers by fine-grained sediment before compression occurred.

SYSTEMATIC PALAEOLOGY

Phylum CNIDARIA Haeckel, 1881

Class HYDROZOA Owen, 1843

Order HYDROIDA Johnston, 1836

Suborder CHONDROPHORINA Chamisso and Eysenhardt, 1821

Family CHONDROPLIDAE Wade, 1971

Genus PALAELOPHACMAEA Donaldson, 1962

Type species. Palaelophacmaea criola Donaldson, 1962.

Diagnosis. Subcircular low cone with distinct radial ridge extending to margin and irregular concentric corrugations with finer growth lines on each. No indication of sail structure.

Palaelophacmaea annulata (Yokoyama)

Plate 10, figs. 1-6

1890 *Capulus annulatus* Yokoyama, pl. 25, fig. 17a, b.

1963 *Brunonia? annulata* (Yokoyama); Matsumoto *et al.*, pl. 51, fig. 17.

1975 *Anisomyon annulatus* (Yokoyama); Kanie, pl. 19, figs. 3, 4a, b.

1977 *Anisomyon annulatus* (Yokoyama); Kanie, pl. 2, fig. 7.

EXPLANATION OF PLATE 10

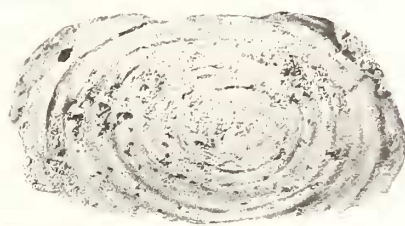
Figs. 1-6. *Palaelophacmaea annulata* (Yokoyama), Ishido Formation. All specimens whitened with MgO. 1, NSM PM1246a, cast showing low, flattened shape and irregular but concentric corrugations interpreted as flattened pneumatocysts. Note original radial ridge is also flattened to produce a furrow, $\times 1.2$, Loc. Sa307. 2, YCM GP548, $\times 1$, loc. Sa203. 3, YCM GP552, small, oval specimen showing concentric corrugations but without any clear signs of a radial ridge, $\times 1.66$, loc. Sa203. 4, NSM PM1249, details of central area and suspected central pore. Note coarse pustulose granules, $\times 2.2$, loc. Sa231. 5, NSM PM1249, almost complete, highly convex specimen, illustrating the distinct radial ridge and central apex. Note finer 'growth lines' and irregular outer margin characterized by flexure of the lower left side, $\times 1.25$, loc. Sa231. 6, YCM. GP549, illustrating the irregularities of the concentric pneumatophore, offset radial ridge, and irregularities of the margin, $\times 2$, loc. Sa203.



1



2



3



4



5



6

Material. Description based on five well-preserved specimens showing both interior and exterior: YCM GP548, YCM GP549, YCM GP552, NSM PM1246 a, b, and NSM PM1249, housed in the National Science Museum (NSM), Tokyo and in the Yokosuka City Museum (YCM), Yokosuka, Japan.

Description. Low, circular to oval bilateral shields or cones, 1–3 cm high with irregularly spaced concentric corrugations (pneumatocysts) ending in sharp apical ring. Pneumatocysts slightly overlapping and 1–3 mm thick. Finer concentric lines superimposed on pneumatocysts, about five to twenty on each one. Pneumatophore disc usually thin and compressed with a distinct, raised radial ridge extending from apex to margin to produce bilateral symmetry. A very faint, fine granular texture occurs over surface of most fossils while others are smooth, suggesting that a thin film-like covering was present. Outer margin flat and irregular, possibly deflected at contact with radial ridge.

Discussion. One of us (Y.K.), has examined the type of Yokoyama (Bayerische Staatssammlung, Munich, West Germany) and found that it agrees precisely with our material. The most distinctive aspects of the specimens are the radial ridge and somewhat irregularly arranged, concentric corrugations of the pneumatophore disc. The preserved configuration of the disc ranges from conical to flattened depending on the degree of compression. The expanding radial ridge is plastically deformed and offset in one specimen (Pl. 10, fig. 6) suggesting an originally chitinous pneumatophore. Another specimen (Pl. 10, fig. 2) shows coarse, less distinct corrugations and surface details, suggesting that it is an interior cast of the pneumatocysts. All specimens show some distortion, especially flattening. Plate 10, figs. 4, 5 show a complete, centrally located, sharp apex formed by a single ring-like corrugation and central pore. The surface is characterized by a fine pustulose texture with finer lines superimposed on the broader corrugations of each pneumatocyst. One broken specimen (Pl. 10, fig. 1) shows a smooth, thin, almost film-like surface.

SYSTEMATIC POSITION AND AFFINITIES

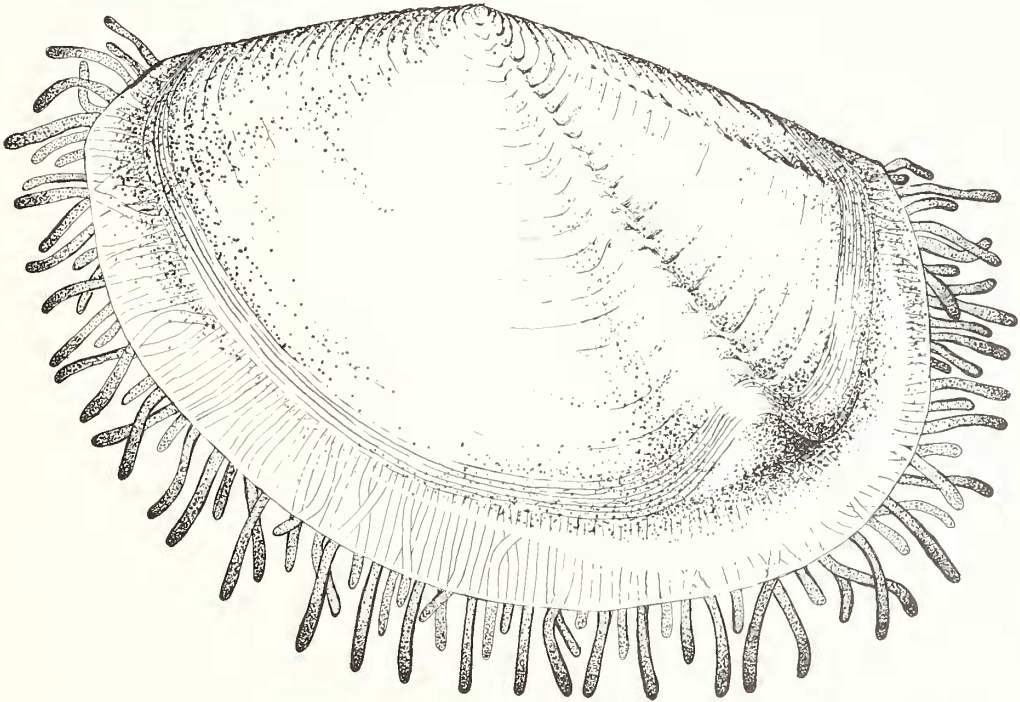
The species *Anisomyon annulatus* was described as a patelliform gastropod by Yokoyama (1890, p. 200, pl. 25, figs. 1–7a, b) and originally designated *Capulus annulatus*. Yokoyama's specimen was again illustrated as a patelliform gastropod by Matsumoto *et al.* (1963) and conspecific material was similarly described and illustrated by Kanie (1975, 1977). Based on our re-evaluation of these specimens, all the fossils of this species must be transferred from Mollusca to Cnidaria (Hydrozoa).

Palaeophacmaea was described by Donaldson (1962) as an enigmatic limpet-like patelliform gastropod from the lower Ordovician of central Pennsylvania, U.S.A. (type species *P. criola* Donaldson). Donaldson's specimens were reillustrated by Yochelson and Stanley (1981) and on the basis of comparative study with Devonian chondrophorines, they assigned *Palaeophacmaea* to the chondrophorine hydrozoans. The similarity between Donaldson's specimens and *A. annulatus* (Yokoyama) is so striking in all aspects that we are forced to reassign this species to *Palaeophacmaea*. As outlined in Yochelson and Stanley (1981) features such as the irregularity of the concentric corrugations, evidence of plastic deformation, and the thin, film-like nature of the 'shell' are not characteristic of a mollusc shell but more compatible with the convex, internal, chitinoid pneumatophore of a chondrophorine hydrozoan. Although fossil chondrophorines were first recognized by Ruedemann (1916), details of these fossils were not known until the work of Caster (1942). They are still usually regarded either as problematica or confused with a variety of unrelated organisms. The apparent similarity of their compressed float structure with univalved mollusc shells is particularly striking.

Kanie (1975, pp. 27–29, pl. 19, figs. 3 and 4a, b; 1977, pl. 2, fig. 7) described and illustrated specimens of *A. annulatus* (Yokoyama) in a monograph and paper on Cretaceous patelliform gastropods from the northern Pacific and compared them with the type illustrated in Matsumoto *et al.* (1963). Kanie (1975) noted the unusual thinness of the shell and the absence of muscle scars in all specimens of *A. annulatus*. In discussing the relationship with other Cretaceous species of patelliform gastropods, Kanie (1977, p. 60) noted the questionable nature of Yokoyama's specimen.

Absence of muscle scars is an important criterion for distinguishing the chondrophorine pneumatophore from the shells of univalved molluscs. Yochelson *et al.* (1983) reviewed the biology and anatomy of lower Devonian chondrophorines, providing additional clues for their recognition. These include: (1) evidence of plastic deformation of the originally pliable chitinoid pneumatophore which is readily subject to deformation, especially crushing, without fracturing, (2) irregularities of the concentric corrugations and the distinctive radial ridge or groove, and (3) the exceedingly thin nature of the compressed pneumatophore which is quite different from thicker, calcitic material of mollusc shells. In addition to the above criteria, the occurrence of suspect fossils in environments generally uncharacteristic for some molluscs, such as deep pelagic sediments, might also prove useful. Chondrophorines, being planktonic wind-dispersed organisms, can occur in all facies types, but most frequently occur in association with exclusively pelagic or deeper water benthic faunas.

P. criola and *P. annulata* differ from all other taxa and cannot be assigned to either of the two chondrophorine families Velellidae and Porpitidae (Harrington and Moore 1956). The Velellidae, such as *Plectodiscus*, like *Palaelophaemaea* are bilaterally symmetrical but display a distinct sail rising from the pneumatophore disc or cone. The Porpitidae, on the other hand, lack a sail and are radially, not bilaterally, symmetrical by virtue of numerous radial partitions within the circular pneumatophore. *P. annulata* and *P. criola* lack a sail but they possess bilateral symmetry and concentric pneumatocysts rather than radial partitions like the Porpitidae (text-fig. 3). The raised ridge of *P. annulata* is not a structure homologous with the velellid sail but, like other chondrophorines, most likely accommodated a major vascular vessel that crossed the soft



TEXT-FIG. 3. Reconstruction of *Palaelophaemaea annulata* shown in floating position. Reconstruction illustrates the convex pneumatophore disc that during life was secreted within the coenosarc of the hydrozoan. Arrangement and positions of the tentacles and other soft parts is based on those of *Porpita* and *Veleva*.

coenosarcal tissues in which it was imbedded. Although characteristics of *P. annulata* do not allow its placement in any living chondrophorine family, they do agree with Precambrian bilaterally symmetrical chondrophorines from the Ediacara fauna for which Wade (1971) erected the family Chondroplidae. We therefore assign *P. annulata* to this extinct family. In doing so we not only establish *P. annulata* as the first Mesozoic chondrophorine, but also extend the range of the family from the Pre-Cambrian to the Cretaceous, with only one other occurrence in the Ordovician (Yochelson and Stanley 1981). Continued search may reveal further examples within this extensive interval of time. This still leaves open the question of why representatives of the two extant families, Porpitidae and Velellidae, have not yet been found in post-Carboniferous strata. Because few palaeontologists are familiar with these fossils, discovery and proper identification of other examples hinges on understanding conventional chondrophorine morphology and establishing multiple, working criteria to distinguish such fossils from morphologically similar but unrelated molluscan taxa. Based on the conservative nature of their evolution and their wide stratigraphic range, one should expect to find closely similar genera and species occurring throughout the Phanerozoic.

Acknowledgements. We thank Mr. K. Takei (Kosei High School, Tokyo), Dr. M. Matsukawa (Ehime University), and Mr. H. Tsuda for collecting and donating the chondrophorine specimens for our study. Dr. E. L. Yochelson first recognized the problematic nature of our specimens and the possibility that they could be chondrophorine pneumatophores rather than univalved molluscs. We are grateful to him for earlier discussions concerning the affinities of our material as well as reviewing an earlier draft of our manuscript. Ms. R. Jumer (Missoula) skilfully drafted the reconstruction in text-fig. 3.

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NOTE ADDED IN PROOF

Additional specimens from the Ishido Formation described as *Brunonia annulata* (Yokoyama) and as a new species *B. undulata* Kase, appeared in publication while this paper was in press. The former specimens (Kase 1984, pl. 3, figs. 8–10) are judged by us to be *Palaelophacmaea annulata* (Yokoyama). The latter (Kase 1984, pl. 3, figs. 6a, b, 7a, b) may also be referred to *Palaelophacmaea*.

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Typescript received 24 January 1984

Revised typescript received 25 April 1984